学位申請論文

清水大輔

Relationship between tooth wear and chewing efficiency in red colobus (*Procolobus badius*).

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Abstract

The purpose of this paper was to describe the wear pattern, length of cutting edges, and shape of the enamel edges on M_2s of *Procolobus badius oustaleti* (red colobus) in the various stages of wear, and to try to relate the observed characteristics with their chewing function. The dentine exposure is not formed on the slopes of basins, but on the ridges of lophs and crests. The bucco-lingual cross-sections of enamel edges are trapezium in shape with very narrow top like a triangle. These shapes are not change with progression of wear. And three cross-sections (through mesial cusps, through lingual notch and median buccal notch, and through distal cusps) of enamel edges in an individual are formed the same shape. As the buccal crests and the enamel edges are considered the cutting edges, the length of the cutting edges hardly changes until the molar crown is considerably worn (over the 75% of the relative dentine exposed value). This combination of attributes indicates that enamel edges formed on the buccal margin keep the same shape and length during an extended period of their life, and serve to maintain the functions of shredding and shearing as wear progresses.

Introduction

The function of primate teeth has been discussed primarily focused on the occlusal morphology of unworn teeth. Species that possess high relief molar crowns accompanying with high cusps, like colobines, are specialized for more folivorous diets, while species that possess low relief molar crowns with low, rounded cusps, like cercopithecine are more omnivorous or frugivorous (Kay & Hiiemae, 1974; Lumsden & Osborn, 1977; Hartman, 1988; Spears & Crompton, 1996). Colobine has longer molar ridges than in cercopithecines (Kay, 1978; Kay & Hylander, 1978; Benefit, 1987). Folivores must have a higher shearing potential of tooth than frugivores. Further, among fruit-eaters, specialists for hard food items have even a lower shearing potential of tooth and blunter teeth than species which more depend on soft fruits (Kay & Covert, 1984; Anthony & Kay, 1993; Meldrum & Kay, 1997). It has been pointed that a positive correlation exists between the length of ridges and the intake of leaves even within the Colobinae (Kay, 1978; Kay & Hylander, 1978; Teaford, 1983).

The length of cutting enamel edges of the occlusal surface has been focused in relation to chewing effectiveness in various mammal species. In folivores common ringtail possum (*Pseudocheirus peregrinus*), koala (*Phascolarctos cinereus*) and eastern (*Macropus gigantesu*) and western grey kangaroos (*Macropus fuliginosus*), the cutting edges function like blades on food, and a strong positive correlation is suggested between the length of the cutting edges and chewing effectiveness (Resberger, 1973;

Gipps & Sanson, 1984; Lanyon & Sanson, 1986; McArthur & Sanson, 1988). Thus, influences of the occlusal shape change following dentine exposure on the chewing effectiveness has been discussed in various mammals. Lanyon & Sanson (1986) and McArthur & Sanson (1988) pointed that the total length of the cutting edges increases after wear. And these authors suggested that chewing function is improved by tooth wear. In general, occlusal wear increases the areas of tooth contact, therefore, tooth effectiveness increases after the enamel cusps have worn off (Osborn & Lumsden, 1978; Hillson, 1986; Wilding, 1993).

Primate molars are not replaced by succedaneous teeth even after heavily worn. The permanent teeth need to maintain functional efficiency for food breakdown throughout the lifetime. As an adaptation for the breakdown of hard food, for example, thick enamel resists dentine exposure as the wear proceeds and allows flattening of the occlusal surface for more effective grinding and crushing (Benefit, 1987). If so, what advantage does thin enamel have in worn teeth whose dentine is exposed? Gordon (1980) has suggested sharpened enamel rims which are formed around the exposed dentine basin serve to crush or shred the fibrous food in thin-enameled chimpanzees. However, study of tooth wear pattern focusing on influence on the masticatory function are rare. Ungar & Williamson (2000) have explored the effects of tooth wear by dental topographic analysis. In this study, they pointed an importance of shapes of worn teeth, especially of a significance of sharp edges produced by dentine exposure for efficient shredding and slicing abilities.

In this paper, I describe morphological features of the enamel rims which are formed by the dentine exposure proceeds in folivorous red colobus (*Procolobus badius oustaleti*) and estimate the functional significance of the cutting edge. In many folivorous or herbivorous mammals, the masticatory effectiveness of molars is achieved and maintained by dental alteration through wear (Lanyon & Sanson, 1986; McArthur & Sanson, 1988). I quantitatively examined the length of the cutting edges in various stages of tooth wear and discuss the nature and possible effects of tooth wear.

P. badius is one of the most specialized folivores among living primates. Unfortunately, food composition data about *P. b. oustaleti*, subject in this sutdy, is not available. I show, however, data for *P. b. tephrosceles* on Kibale Forest, western Uganda and *P. b. badius* on Tiwai Island, Sierra Leone, as a reference. In *P. b. tephrosceles* on Kibale Forest, western Uganda, leaf parts comprises over 70% of the diet (Struhsaker, 1978), including 14.5% leaf buds, 27.15% young leaf parts, 23.65% mature leaf parts, and 8% leaves of unknown age. *P. b. badius* on Tiwai Island, Sierra Leone consumes diet consisting of 20% mature leaf parts, 32% young leaf parts, 16% flowers, and 31% fruits and seeds (Davies et al., 1999).

Materials and Methods

Materials

Forty-two M_2s of *Procolobus badius oustaleti* were examined. They are 22 males and 20 females at various stages of tooth wear after the third molar has erupted. These specimens are free-ranging individuals collected at Haut-Zaire, Democratic Republic of the Congo, and housed at the American Museum of Natural History, New York.

Terminology

The dental nomenclature used is primarily that of Jolly (1972), Delson (1973), Kay (1977), and Benefit (1987). The terms and their designations are given in Figure 1.

Methods

For measuring, epoxy casts of the specimens were made. Occlusal wear was observed on these casts under the binocular microscope. Occlusal view of each cast was photographed at a magnification of 1:1. Specimens were set so that the cervical plane was parallel to the plane of the camera lens. Two area and two length measurements were taken on the personal computer after scanning the photographs (Figure 2, Table, 1): (1) crown area; (2) area of the dentine exposure; (3) length of the buccal ridges; (4) length of the enamel edges.

The definition of measurements used in this study is as follows (Figure 2, Table, 1). The crown area is the area enclosed by the enamel. The area of the dentine exposure is the sum of all areas of dentine exposure on the tooth crown. The length of the buccal ridges is the sum of paracristid, lateral protocristid, oblique cristid, and hypocristid ridge lengths. In *P. b. oustaleti*, unworn ridge of the buccal crests rises discontinuously from the aspect of basins (trigonid basin, talonid basin, and distal fovea) (Figure 3). Some of rose parts from the aspect of basins discontinuously remained was counted as the length of the buccal ridges. As the lower molars become worn, the dentine is exposed on the buccal cusps and narrow enamel rims are formed around the dentine exposures. The buccal enamel rims are especially well-developed long and sharp. The length of the enamel edges is measured a part of the enamel rims corresponding to the four buccal crests measured about the length of the buccal ridges.

The casts were sectioned through the three lines which passes the lingual notch and the median buccal groove, the protoconid and the metaconid, and the hypoconid and the entoconid perpendicularly to the base of the crown. Each cut face was photographed at a magnification of 1:1, and the image was used to observe and trace a shape of enamel edge in the personal computer.

Results

Observation of wear pattern of red colobus

Wear pattern in the *P. b. oustaleti* molars is recognized six stages as follows (Figure 4). First stage, a mesio-distally narrow band of the dentine exposure is formed on the buccal side of the protolophid slightly lingually of the cusp tip of protoconid. Likewise, on the distal side, a mesio-distally narrow dentine exposure is formed on the buccal side of the hypolophid slightly lingually of the cusp tip of the hypoconid. In second stages, the dentine exposures on the protoconid and hypoconid extend mesio-distally along the buccal crests, and then extend to lingually along the ridges of the lophs. As the dentine exposure progresses from higher points of occlusal relief around cusp tips of the buccal cusps, and along the ridges of the buccal crests and lophs to cervical plane, it is diamond-shaped with the rounded buccal cornered. While the dentine exposure does not reach to the slopes of talonid basin, trigonid basin, and distal fovea, it extends into the ridges of the buccal crests and lophs. As the total area of the dentine exposure account for 10% of the crown area, the third stage, the dentine exposure extends mesio-distally on the ridges of the buccal crest like outstretched arms. In this stage, bucco-lingually narrow bands are formed on the lophs. Also on the lingual half, dentine is never exposed on the slopes of basins. However, a narrow dentine exposure extends toward buccal side on the ridges of lophs. On the buccal half, as the dentine exposure accounts for 20% of the crown area, the forth stage, the mesial part of dentine exposure connects with the distal exposure. In the fifth stage it is connected with the buccal exposed area on the lingual lophs as the crown is exposed by 30% or more in projected area. The dentine exposure progresses along the crests and lophs. In the sixth stage dentine exposure extends the whole of occlusal area (over the 75% of the relative dentine exposed value). The enamel around the lingual notch is the last to wear out.

The length of the buccal ridges

After the complete eruption, the buccal crests begin to function as mastication organ and the wear starts on. The paracristid is first to be worn out, and the lateral protocristid and the oblique crested follows. The hypocristid is last to be worn out. Crests in general wear from the cusp tip side. Figure 5 shows a relationship between the length of the buccal ridges and the dentine-exposing rate. As the exposure accounts for 10% of the crown area, the buccal ridges are completely worn.

Observation of the enamel edges

Figure 6 and 7 show photographs and their tracings of bucco-lingual cross-sections of the enamel-dentine interface in worn molars. The enamel is raised fluently and continuously from dentine basin at the interface. In chimpanzees, these interfaces ocasionally show discontinuity, and form sharp edges (Gordon, 1980; Figure 8). This is not the case for *P. b. oustaleti*. The wearing of the buccal side of the enamel edges is slight. On the occlusal surface of the enamel edges, a very narrow facet is observed. The cross-sections of enamel edges are trapezium with a very narrow top like a triangle. Likewise, on the median cross-sections and the distal cross-sections, the enamel edges are shaped trapezium with a very narrow top like a triangle (Figure 7).

The length of the enamel edges

As the dentine is exposed, enamel rims appear around the dentine exposure. Figure 9 shows a relationship between the length of the buccal ridges and the dentine-exposing rate. The enamel edges are elongated linearly by the exposed area accounts for 20% of the crown area. The total length of the enamel edges reaches about 22mm. At this stage, the mesial part of the exposure connects with the distal exposure and the total length of the enamel edges slightly increases. In stages where the exposed area accounts for 20 to 40% of the crown area, molars have the longest enamel edges. In stages where the exposed area is between 40 to 75% of the crown area, the length of the enamel edges is constant at about 20mm. In later stages, the length of the enamel edges is apparently decreased.

Discussion

From the observation of wear pattern in *P. b. oustaleti*, the dentine exposure is formed on the ridges of lophs and crests, especially on the lingual side of the lower molar crown, bucco-lingually narrow dentine exposures are focused on the lophs. Further, a large amount of occlusal relief on the lingual half remain after the occlusal relief on the buccal half is worn out. These results support the previous study of the wear pattern in colobine monkeys (Walker & Murray, 1975; Teaford, 1983; Benefit, 1987). From the observation of enamel edges, the bucco-lingual cross-sections of enamel edges are trapezium in shape with very narrow top like a triangle. These shapes are not change with progression of wear. And all of the cross-sections in an individual are formed the same shape every part of the enamel edges. In here I try to discuss the chewing functions of the worn tooth in *P. b. oustaleti* from observed characteristic of wear pattern, and the cross-sectional shape of the enamel edges.

Mammalian mastication is explanied from two cycles or phases (see e.g. Hiiemae & Crompton, 1985; Hylander et al., 1987). The initial cycle is puncture-crushing, in which jaw movements are more vertically occurred and the tooth-food-tooth contact happens. The subsequent cycle is chewing or power stroke, in which jaw movements are more horizontally occurred and precise tooth-tooth contacts are possible. In primates, two 'phases' are recognized during chewing. The initial phase involves supero-medial movement of the mandibular molar across the maxillary cusps and thecentric occlusion. This phase is called as the Phase I or the buccal phase. The wear facets in lower molars by Phase I, called shearing facets, are formed on the buccal side of the buccal crests and the buccal slope of the lingual crest (Kay, 1977). The subsequent phase is called as the Phase II or the lingual phase. The mandibular cusps move infero-medially across the maxillary cusps and out of centric occlusion. The wear facets on lower molars by the Phase II mastication, called crashing facets, are formed on the buccal slops of basins (Kay, 1977).

The bucco-lingual cross-sections of enamel edges are trapezium in shape with very narrow top like a triangle. The enamel edges is distributed symmetrically about the directions of jaw movements during the puncture-crushing and Phase I. This characteristic of the enamel edges perhaps accommodates to wedge food particle. A symmetrical triangle about the direction of the applied force is most stable for concentrating the masticatory force on the tips of enamel edges. The concentrated energy is expended as a tension resulting in cracking foods. Cracking runs faster, and foods are comminuted easily. It is suggested that shearing function during the Phase I chewing is less effective since, enamels on the lingual slopes of basins and ridges of the lingual crests of the lower molars in *P. b. oustaleti* remain without dentine exposure. Frequencies and orientation of micro scratches on Phase II facets in clobine molar indicate that the colobines wedge foods at the end of Phase I of chewing. (see Lucas & Teaford, 1994). This supports that the cutting with wedges is major function during Phase I rather than shearing by blades in *P. b. oustaleti.*

During the Phase II, mandibular cusps move infero-medially. The cross-sectional shape of the enamel edge is asymmetric about the direction of jaw movement. When the mandibular buccal cusps and the maxillary lingual cusps pass with each other, two enamel edges contact at one point. As the jaw movement continues, the point of contact moves along the enamel edge. Sequences of such contacts produce efficiently out-of-plane shearing. The micro scratch evidences on the crashing facet also indicate that molars shear foods during the Phase II (Teaford & Walker, 1984).

The lengths of the buccal ridges and of the enamel edges presume the length of cutting edges. Figure 10 plots the length of cutting edges on the relative dentine exposed area. The length of the cutting edges extends from 15-20mm to 20-23mm before the relative dentine exposure accounts for 40%. The length of the cutting edges is maximum around the 40% of the relative dentine exposure. With higher exposed values, especially more than 75%, the length of cutting edges is apparently lowered. The length of the buccal ridges decreased with progressing wear, and completely lost before the dentine exposure comes to account for 10% of the crown area. Because the enamel edges be elongated as substitutes for the buccal ridges, the length of cutting edges do not decrease untill the relative dentine exposed value exceeds 75%.

Because lower molars of *P. b. oustaleti* have a flare, but it is not developed (Delson, 1973; Benefit, 1987), the perimeter of the crown increases following the wearing of the crown. As a result, the cutting edges on the buccal margin increase as dental wear progresses toward the base. The buccal margin of the lower molars has a "w" curve by the median buccal notch. The median buccal notch lies between protoconid and hypoconid. Below the median buccal notch, the buccal face of the crown slopes steeply down to a level roughly halfway to the cervix. This sloping area is the median buccal cleft. Below the median buccal cleft, undulation is greatly reduced and the length of cutting edges decrease. The length of cutting edges is determined by the interaction between flare and the median buccal cleft. Until the area of dentine exposure accounts for 40% of the crown area, the flare has a more strong influence to determined the length of cutting edges, hence cutting edges becomes longer. The median buccal cleft has a stronger influence after the molar crown is considerably worn (over the 75% of the relative dentine exposed value), hence the length of cutting edges decrease.

Cutting edges play a role like blades in food processing. The positive correlation is expected between the length of the cutting edges and chewing effectiveness (Resberger, 1973; Gipps & Sanson, 1984; Lanyon & Sanson, 1986; McArthur & Sanson, 1988). In study of koala (*Phascolarctos cinereus*; Lanyon & Sanson, 1986) or eastern and western grey kangaroos (*Macropus giganteus*, & *M. fuliginosus*; McArthur & Sanson, 1988), the length of the cutting edges of the upper cheekteeth increases as wear progress. The extension of cutting edges related to wear should have an upper limit and decrease beyond its optimum wear level. The length of the cutting edges is related with the chewing effectiveness and consequently with energy requirements in animals. Association between longer ridges and a greater intake of leaves is observed even in Colobinea(Kay,1978、Kay & Hylander, 1978). More folivorous silvered langur (*Trachypithecus cristatus*) has a longer crest than more omnivorous maroon leaf monkey (*Presbytis rubicunda*) (Teaford, 1983). Since *Procolobus* is difficult to raise, there are no zoo specimens with recorded age. Thus, the relationship between teeth wear and age is hard to be evaluated. However, the pattern of increment and decrement of the length of cutting edges in *P. b. oustaleti* provides supportive evidences to the hypothesis about the functional effectiveness in colobine molar morphology.

Summary

The purpose of this paper was to describe the wear pattern, length of cutting edges, and shape of the enamel edges, and to try to relate the observed characteristics with their chewing function in *P. b. oustaleti*. The dentine exposure is not formed on the slopes of basins, but on the ridges of lophs and crests, especially on the lingual side of the lower molar crown, bucco-lingually narrow dentine exposures are focused on the lophs. Further, a large amount of occlusal relief on the lingual half remain after the occlusal relief on the buccal half is worn out. The bucco-lingual cross-sections of enamel edges are trapezium in shape with very narrow top like a triangle. These shapes are not change with progression of wear. And three cross-sections (through mesial cusps, through lingual notch and median buccal notch, and through distal cusps) of enamel edges in an individual are formed the same shape. The length of these enamel edges increases in the early period of the wear stage and decreases in the last period of wear stage. On the other hand the length of buccal edges rapidly decreases in the early period of the wear stage. As the buccal crests and the enamel edges are considered the cutting edges, the length of the cutting edges hardly changes until the molar crown is considerably worn (over the 75% of the relative dentine exposed value). Observed wear pattern and cross-sectional shape of

the enamel edges suggest that the enamel edges can act wedge for food comminuting during puncture-crashing and Phase I of chewing, and act blade during Phase II of chewing. Observed cross-sectional shape of the enamel edges and the length of cutting edges indicate that chewing function is maintained by triangle shape enamel edges existed evenly on the buccal margin of lower molar after dental attrition throughout their life.

Acknowledgments

I thank Prof. Hidemi Ishida, Dr. Masato Nakatsukasa, Dr. Naomichi Ogihara and other staff of the Laboratory of physical anthropology, Kyoto University for their helpful suggestions and insightful comments. I acknowledge helpful discussions with Dr. Yuzuru Hamada, Dr. Toshio Mouri, Dr. Yutaka Kunimatsu, Mr. Takeshi Nishimura and Ms. Michika Kondo of the Primates Research Institute, Kyoto University. My special thanks are due to Dr. Richard Kay of Duke University for valuable advice.

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Table 1. List of measurements (see Figure 2)

Dimension	Definition
Crown Area:	Inside area of enamel outline on the projection images.
Area of dentine exposure:	A sum of all projection areas of dentine exposure to the cervix plane on the tooth crown.
Length of the buccal ridges:	A sum length of paracristid, lateral protocristid, oblique cristid, and hypocristid. Unworn ridge of buccal crests rose discontinuously from the aspect of basins (Figure 2). Some of rose parts from the aspect of basins discontinuously remained after worn off was measured for the length of the buccal ridges.
Length of the enamel edges:	As the lower molars of colobines become worn, the dentine is exposed on the buccal cusps and narrow enamel rims are formed around the dentine exposures. The length of the enamel edges is part of enamel rims equivalent to the four buccal crests measured about the length of the buccal ridges.

Legends of Figures

Figure 1. Location of morphological features on the right lower second molar of *Procolobus badius oustaleti*. A. Occlusal aspect; B. Buccal aspect: a. Protoconid; b. Hypoconid; c. Metaconid; d. Entoconid; e. Paracristid; f. Lateral protocristid; g. Oblique cristed; h. Hypocristid; i. Premetacristid; j. Postmetacristid; k. pre-entocristid; l. medial postentocristid; m. Protolophid; n. Hypolophid; o. Trigonid basin; p. Talonid basin; q. Distal fovea; r. Mesial buccal cleft; s. Median buccal cleft; t. Distal buccal cleft; u. Lingual notch; v. Median buccal notch. Grooves are represented by interrupted lines; crests and ridges by solid lines.

Figure 2. Measured dental feature. A. Occlusal view of unworn lower second molar. Thick lines show paracristid, lateral protocristid, oblique cristed, and hypocristid measured as the length of buccal crests. B and C. Occlusal view of worn lower second molar. Thick lines of figure A are measured as the length of the enamel edges. Black areas in figure C are measured as the area of dentine exposure. Crown area is both gray and black areas in figure C. Grooves are represented by interrupted lines; crests, ridges and enamel edges by solid lines.

Figure 3. Oblique view of unworn lower second molar of *Procolobus badius oustaleti* shows that unworn ridge of the buccal crests rises discontinuously from the aspect of basins.

Figure 4. Wear stages. A is the first stage, and the relative dentine exposed value is 0.54%. B is the second stage, and 3.93% exposed. C is the third

stage, and 13.18% exposed. D is the forth stage, and 19.94% exposed. E and F are the fifth stage, and each relative dentine exposed value is 34.52% and 46.76%. G and H are the sixth stage, and each relative dentine exposed value is 83.43% and 90.06%. Dentine exposed areas are represented by gray mask; grooves by interrupted lines; crests, ridges and enamel edges by solid lines.

Figure 5. Length of the buccal crests (mm) plotted against dentine-exposing rate.

Figure 6. Photographs and tracings of cross-sections through the mesial cusps show the shape of enamel edge. A is the second stage. B is the third stage. C is the forth stage. D is the sixth stage.

Figure 7. Photographs and tracings show the shape of enamel edges of an individual that is forth stage. A is a cross-section through the mesial cusps. B is through the lingual notch and the median buccal notch. C is through the distal cusps.

Figure 8. Tracing of the broken edge of an enamel edge of chimpanzee. E shows enamel and D shows dentine. It is taken from Gordon 1980.

Figure 9. Length of enamel edges (mm) plotted against dentine-exposing rate.

Figure 10. Length of cutting edges (mm) plotted against dentine-exposing rate.

Figure 1

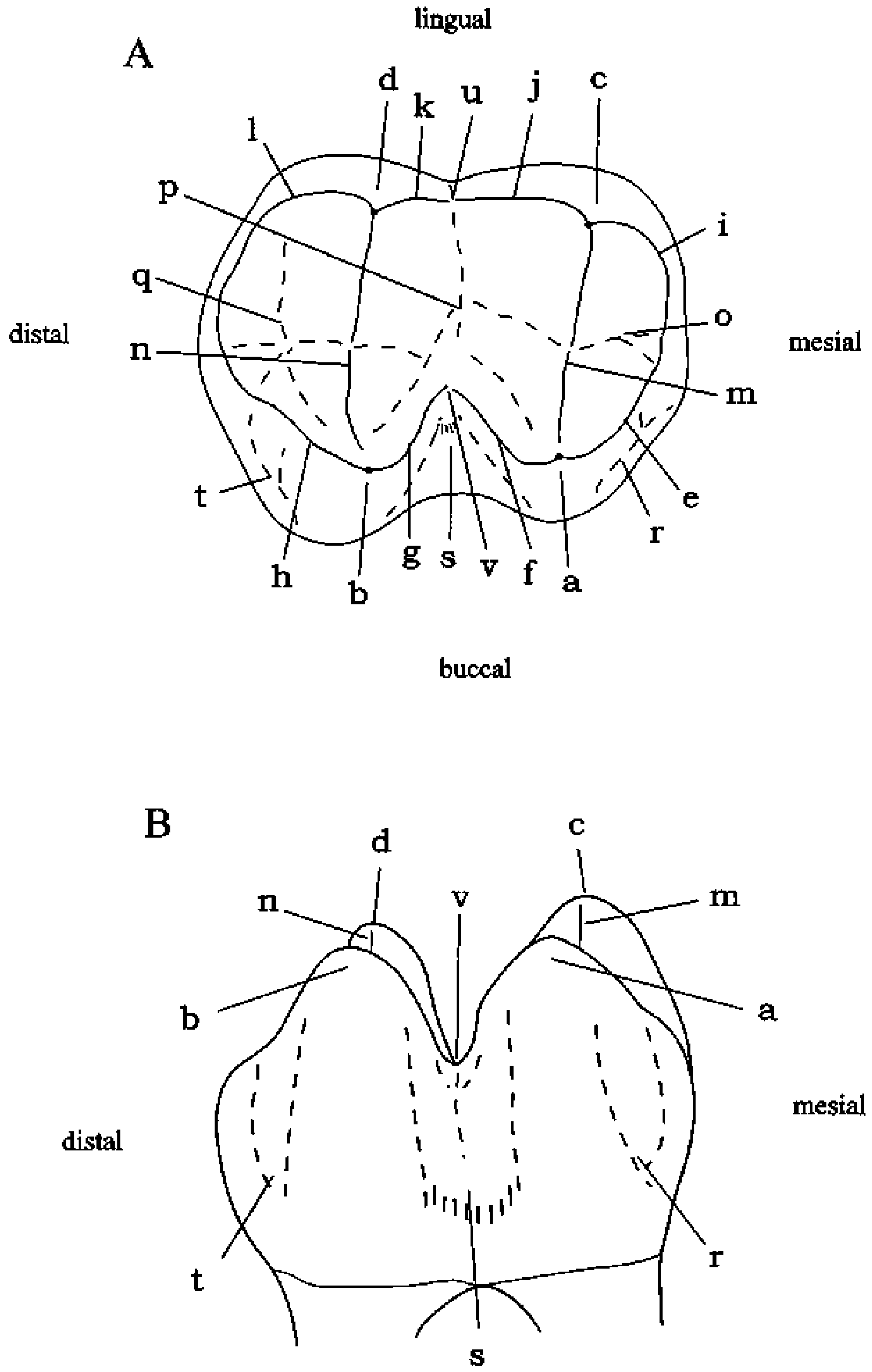
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Figure 2

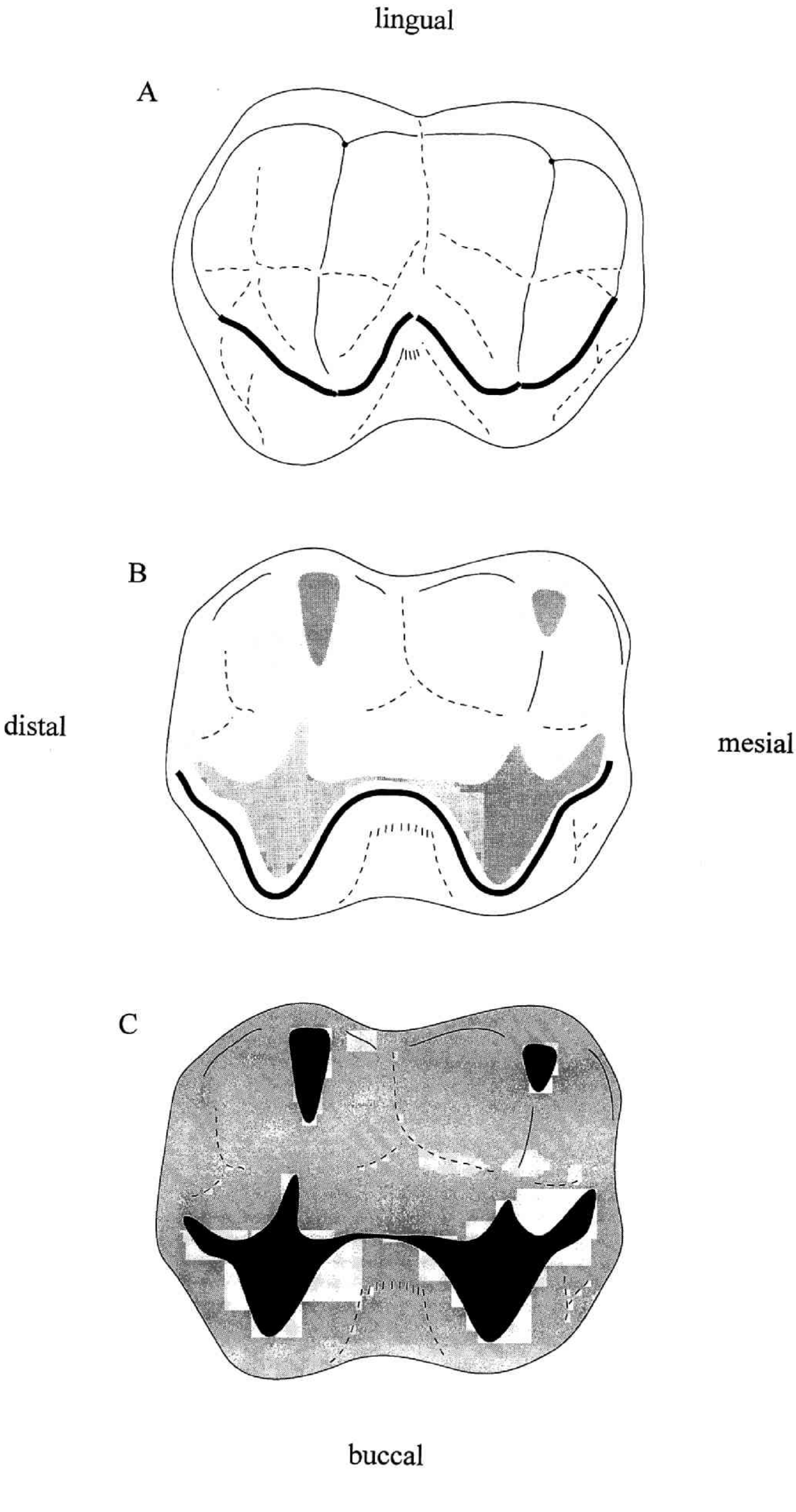


Figure 3

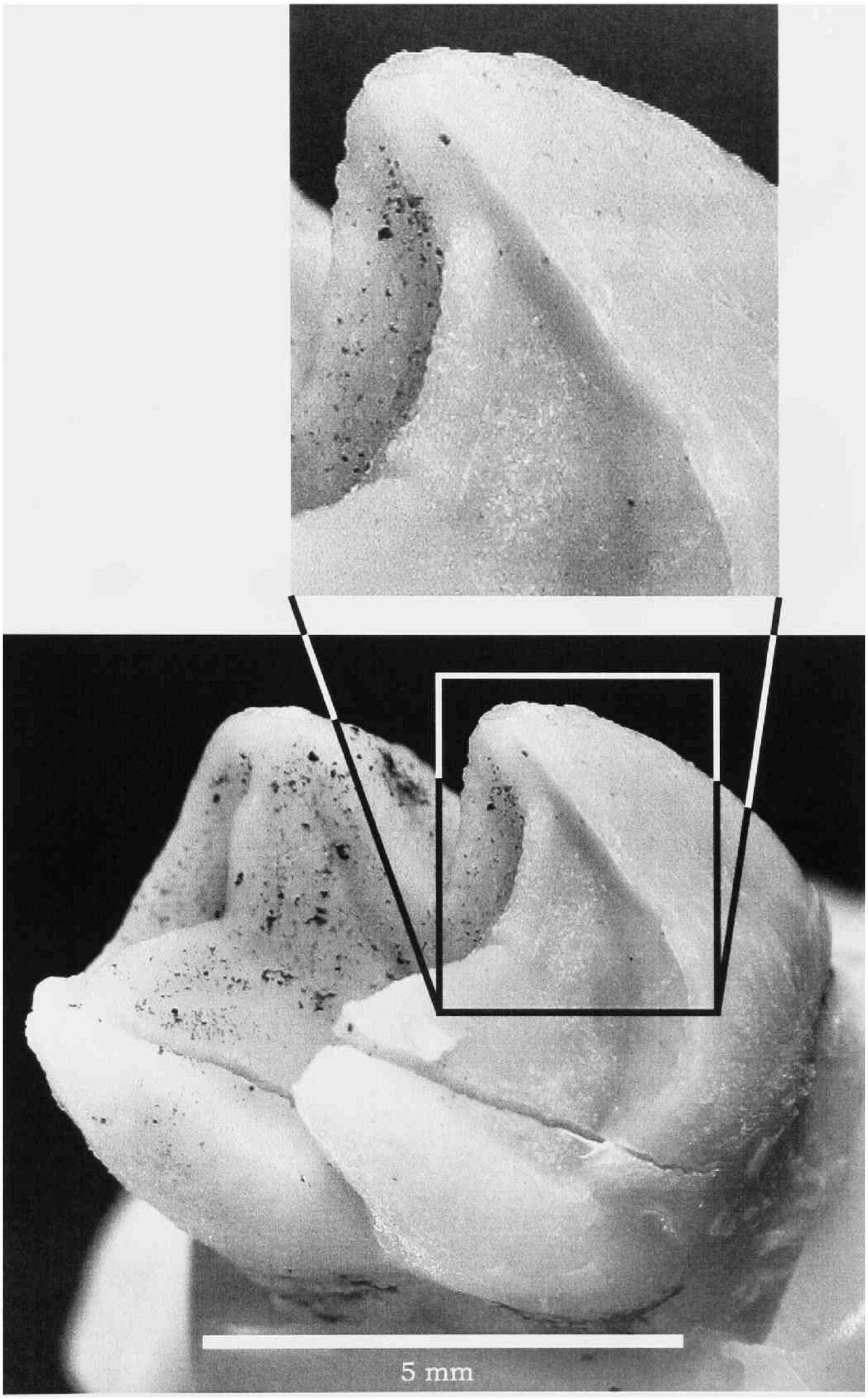


Figure 4

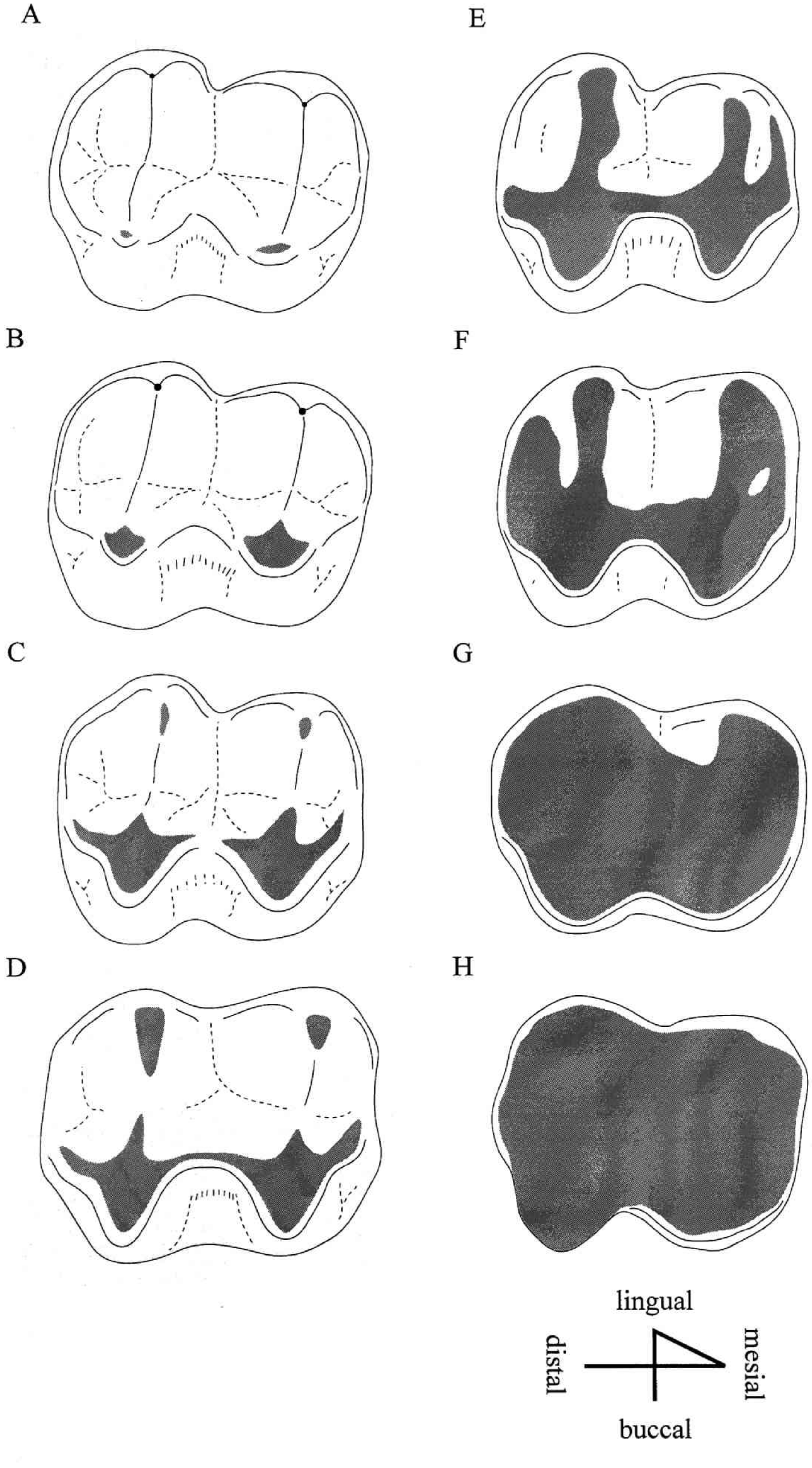
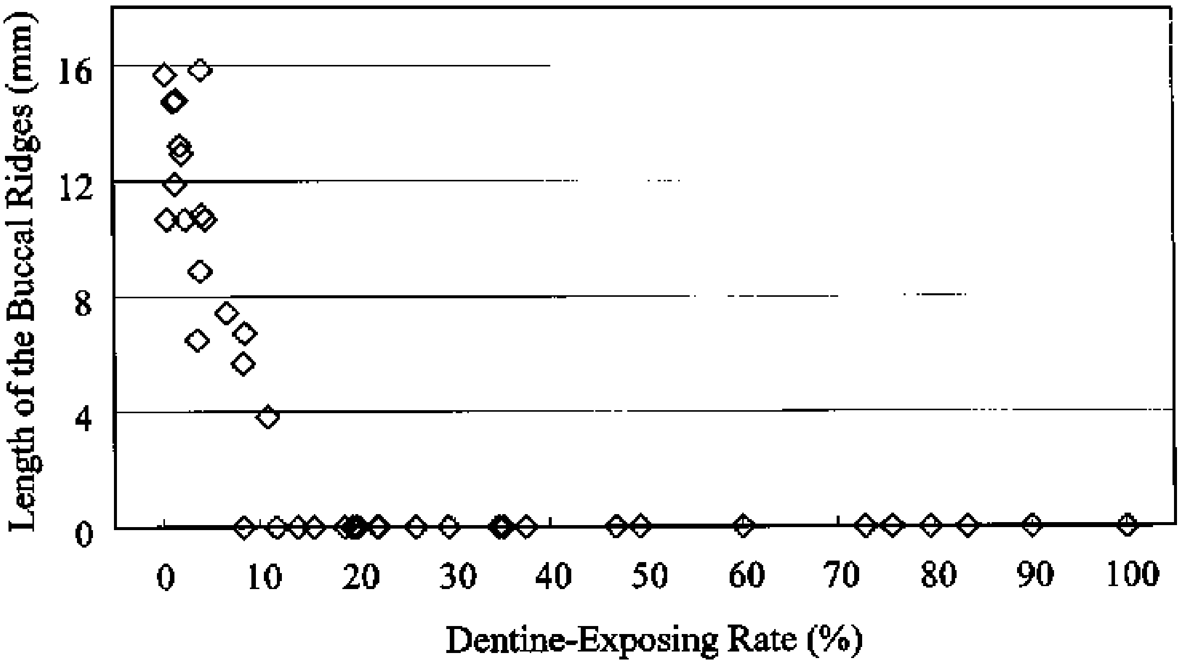


Figure 5



Length of the Buccal Ridges (mm)
16
12
8
4
0
0
10
20
30
40
50
60
70
80
90
100
Dentine-Exposing Rate (%)

Figure 6

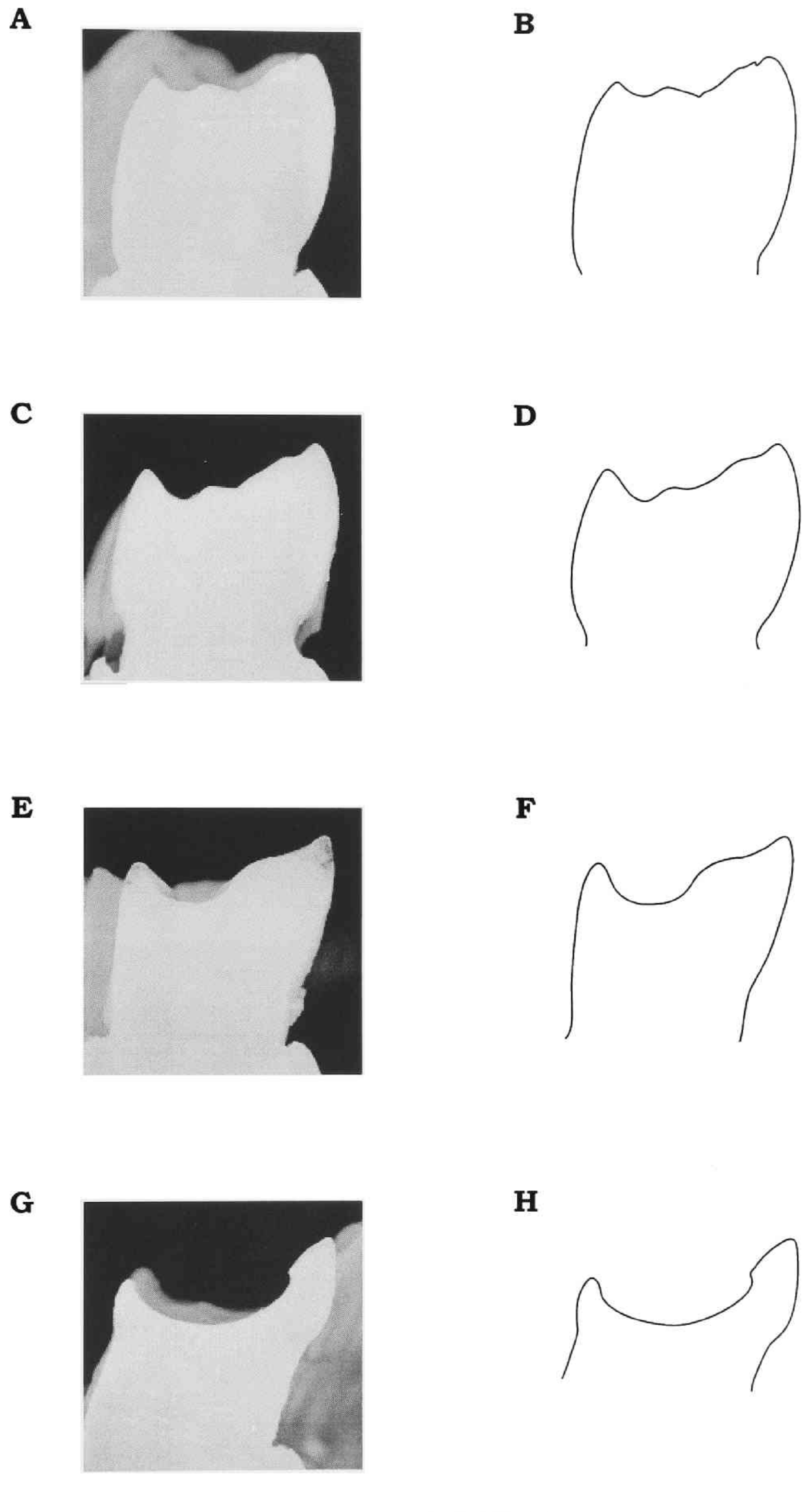


Figure 7

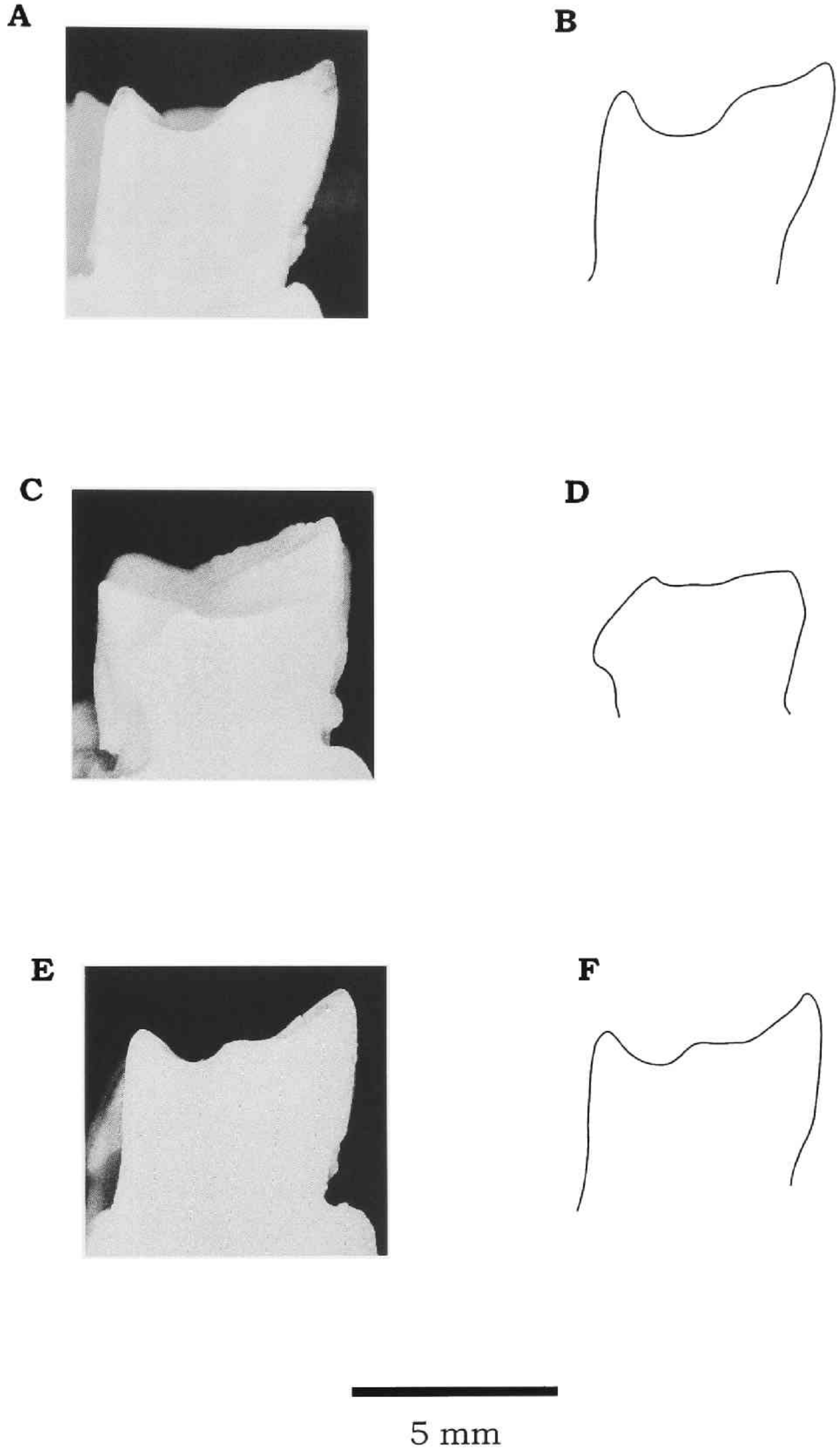


Figure 8

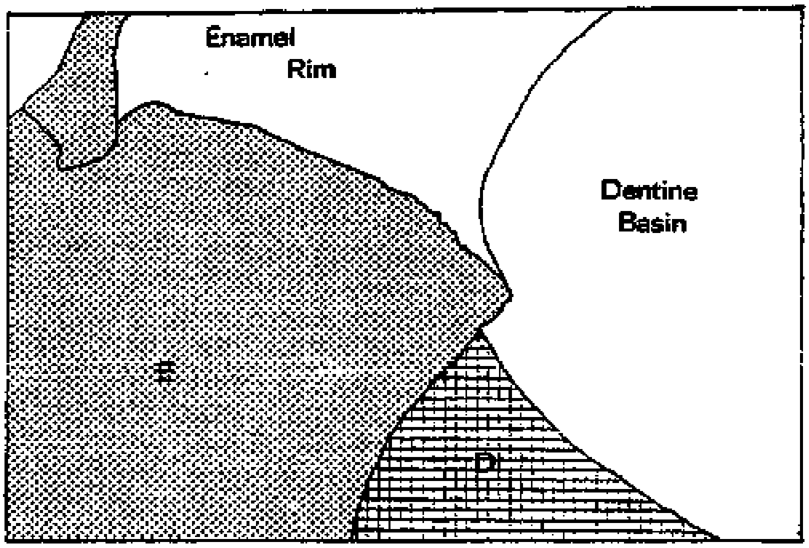
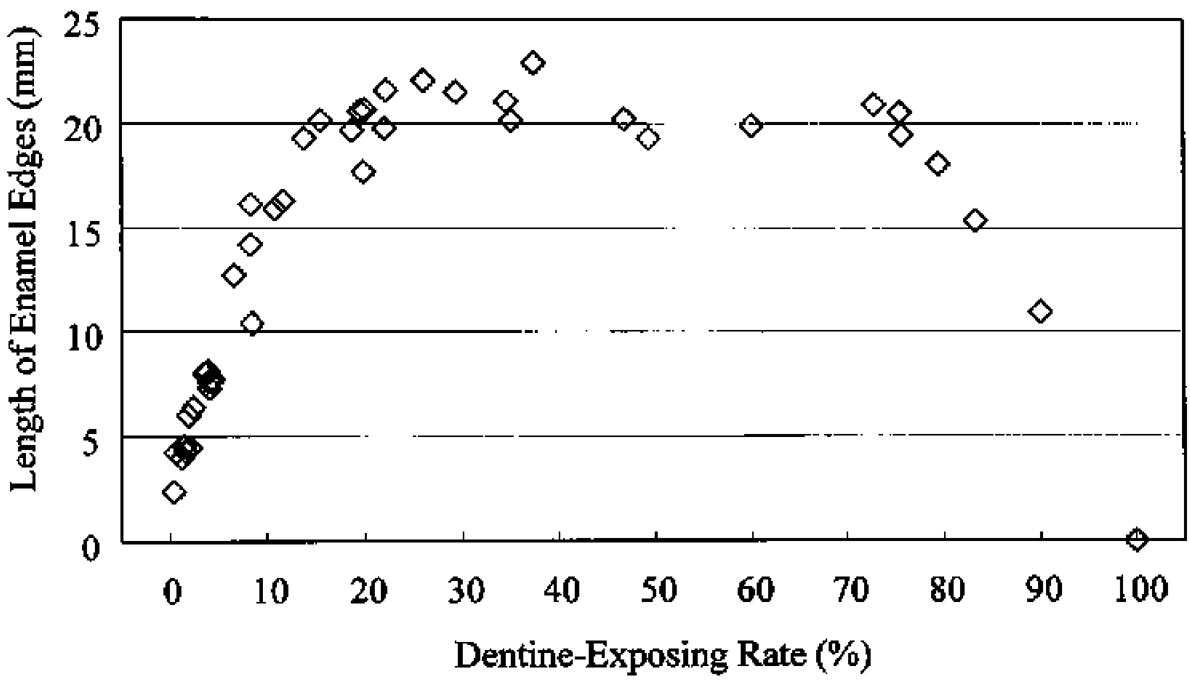
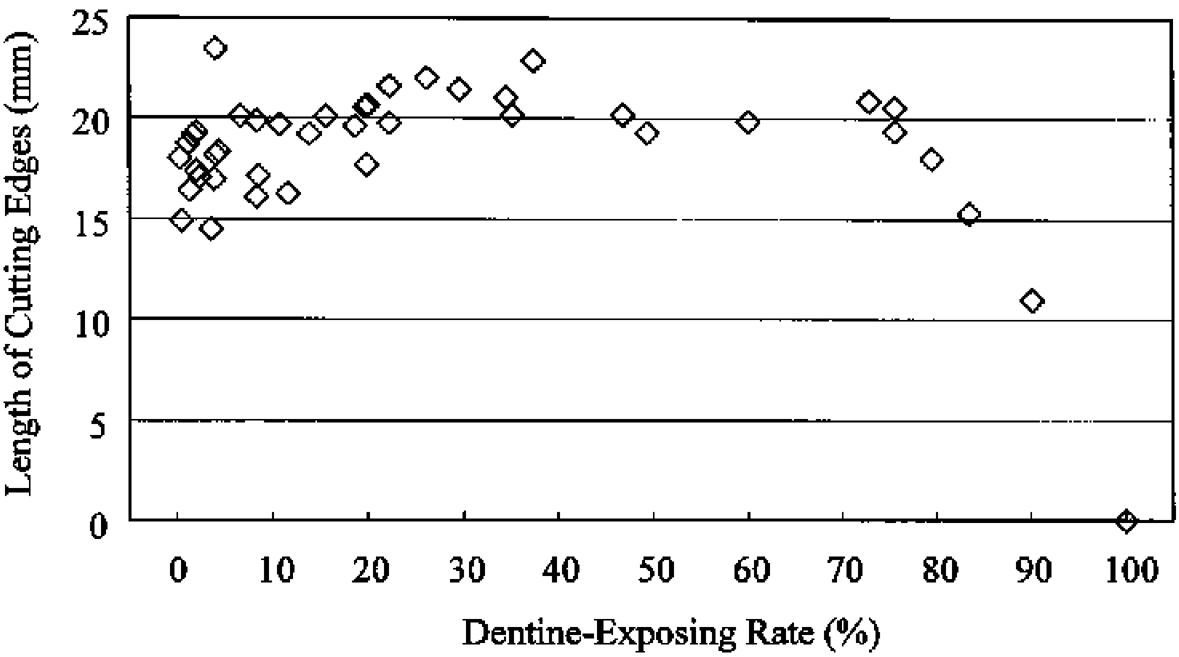


Figure 9



Length of Enamel Edges (mm)
25
20
15
10
5
0
0
10
20
30
40
50
60
70
80
90
100
Dentine-Exposing Rate (%)

Figure 10



25
20
15
10
5
0
Length of Cutting Edges (mm)
0
10
20
30
40
50
60
70
80
90
100
Dentine-Exposing Rate (%)

Functional implications of enamel thickness in the lower molars of red colobus (*Procolobus badius*).

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Abstract

The purpose of this study is to compare the pattern of enamel distribution on unworn M_2s of folivorous (*Procolobus badius*: red colobus) and omnivorous (*Macaca fuscata*: Japanese macaque) primates, and to try to relate the observed differences to their dietary behavior. As the lower molars of colobines become worn, the dentine is exposed on the buccal cusps and narrow enamel rims are formed around the dentine exposures. The buccal enamel rims are especially well-developed and sharp, a pattern that has been selected for as being advantageous for shredding fibrous plant materials. The results of this study demonstrate that the enamel on the lingual side of the protoconid, where dentine exposure occurs first, is much thinner in *P. badius* than it is in *M. fuscata*. In addition, the dentine is exposed and thin enamel rims are formed faster in *P. badius* than in *M. fuscata*. Also, *P. badius* has significantly thinner enamel and a higher protoconid and metaconid. The angle between the cervical plane and the buccal slope is significantly higher in *P. badius* (74°) compared with *M. fuscata* (55°). The steep buccal surface and thinner enamel of *P. badius* enable this species to maintain narrow rims even after dental attrition, while the high cusps of the molars may be an adaptation for providing narrow enamel rims throughout life.

Introduction

The function of primate teeth has been discussed primarily in relation to occlusal morphology and enamel thickness. Species that possess high relief molar crowns with high cusps, like colobines, are adapted for more folivorous diets, while species that possess low relief molar crowns with low, rounded cusps, like macaques, are more omnivorous or frugivorous (Kay & Hiiemae, 1974; Lumsden & Osborn, 1977; Hartman, 1988; Spears & Crompton, 1996). In general, thick enameled molars, found in hard object feeders, are more resistant to exposure of the dentine at the cusp tips, and when worn they form a flatter occlusal surface. Sharper crests on thin enameled molar, typical of folivores, are most efficient for shearing tougher, fibrous foods and the dentine becomes exposed more quickly. Patterns of enamel distribution on the occlusal surface are affected by various functional and mechanical demands. For instance, "supporting cusps" (i.e., the protocone and protoconid) with greater masticatory loading have thicker enamel than "guiding cusps" (i.e., the paracone and metaconid) to resist wear (Gantt, 1977; Molnar & Gantt, 1977; Macho & Berner, 1993, 1994).

Molars of primates are not replaced by succedaneous teeth when heavily worn. As a consequence, the permanent teeth need to maintain functional efficiency for food breakdown throughout the lifetime of an individual. For example, as an adaptation for the breakdown of hard food items throughout an individual's lifetime, thick enamel resists dentine exposure after wear and allows flattening of the occlusal surface for more effective grinding and crushing (Benefit, 1987). What adaptive advantage does thin enamel have when the dentine is exposed? Gordon (1980) has suggested that in thin-enamelled chimpanzees, sharp enamel rims around the exposed dentine basin serve to crush or shred the food. However, there has been no detailed study of tooth wear patterns and their functional effects on mastication. Ungar & Williamson (2000) have explored the effects of tooth wear on functional morphology using dental topographic analysis. In this preliminary study, Ungar & Williamson demonstrate the importance of studying the shapes of worn teeth, especially the significance of sharp edges produced by dentine exposure as a way to improve shredding and slicing abilities.

In this paper I describe differences in the pattern of enamel distribution between folivorous and omnivorous primates, and try to relate these difference to their diet. Furthermore, I attempt to assess the functional consequences of wear in molars of folivorous monkeys with thin enamel. In particular, I focus on whether the sharp enamel rims that form after dentine exposure function as cutting edges, analogous to the occlusal morphology seen in selenodont artiodactyls in which functionality is achieved and maintained by dental alteration through wear (Lumsden & Osborn, 1977). Previous studies have shown that cutting edges act as blades for comminuting food and that dentine exposure is an important factor in maintaining the functional effectiveness of the occlusal morphology (Rensberger, 1973; Lanyon & Sanson, 1986).

In this study I compare the lower molars of red colobus (*Procolobus badius*), one of the most specialized folivores among living primates, with those of the omnivorous Japanese macaque (*Macaca fuscata*). *Procolobus badius* on Tiwai Island, Sierra Leone has a diet consisting of 20% mature leaf parts, 32% young leaf parts, 16% flowers, and 31% fruits and seeds (Davies *et al.*, 1999). In Kibale Forest, western Uganda leaf parts comprise over 70% of the diet (Struhsaker, 1978), including 14.5% leaf buds, 27.15% young leaf parts, 23.65% mature leaf parts, and 8% leaves of unknown age. *Macaca fuscata* on Yakushima Island, Japan has a diet consisting of 76% fruits, 18% leaf parts, and 3% invertebrate (Maruhashi, 1980).

Materials and Methods

Materials

Eight M_2s of *Procolobus badius* (3 unworn, 5 slightly worn) and six unworn M_2s of *Macaca fuscata* were used in this study. The *P. badius* material consisted of five females and three specimens of unknown sex. All of the *M. fuscata* specimens were females. These specimens are housed at the Primate Institute of Kyoto University, Inuyama.

CT scanning

These specimens were scanned by using a pQCT scanner (peripheral quantitative computed tomography: XCT Research SA+, Norland & Stratec Co.) at the Laboratory of Physical Anthropology, Kyoto University. I scanned the specimens with a tube voltage of 49.9 kV and a tube current of 0.45mA. The thickness of the slice and the interval of the adjacent slice were both 0.1 mm. The pixel size was 0.1mm and each CT image had a pixel matrix of 202 × 202. It took approximately 10 hours to scan each tooth. Specimens were mounted on a wooden stage using adhesive tape so that the cervical plane was perpendicular to the plane of the line of X-ray beams.

Determination of the boundary between different materials or between the air and solids can be problematic in analyzing CT images. CT values change gradually from one level to another at such a boundary, rather than intermittently (Figure 1). In the case of Figure 1, for example, the actual boundary is difficult to determine. In this study, I adopted the criterion known as a half maximum height (HMH), in which the median of two CT number levels was conventionally regarded as the boundary between different materials (Koehler *et al.*, 1979; Spoor *et al.*, 1993; Ohman *et al.*, 1997).

In CT images of a tooth, the air-enamel, air-dentine, and enamel-dentine boundaries must be determined. However, the lower thresholds of enamel calculated from the HMH values were different at the air-enamel and enamel-dentine boundaries. The HMH value at the air-enamel boundary is always lower than that at the enamel-dentine boundary. If the former value is adopted as the lower threshold of enamel it results in an overestimation of the enamel thickness at the dentine-enamel junction (DEJ). On the other hand, if the latter value is chosen as the lower threshold of enamel, CT values that are lower than this value and higher than the HMH value at the true air-dentine boundary are recognized as dentine (Figure 1). This results in the operational formation of non-existent dentine, partly on the outer surface of enamel. Thus, I determined the lower thresholds of enamel at the air-enamel boundary and dentin-enamel boundary independently (Yamanaka *et al.*, 2001) (Figure 2).

Measurements

For the three dimensional (3-D) reconstruction of the tooth, the Application Visualization System (AVS, Stardent Computer Inc.) was used on a workstation (Silicon Graphics Octane). Each 3-D reconstructed tooth was resliced to obtain linear measurements on the anatomically determined plane that passes through the apices of the dentine horns of the mesial cusps perpendicular to the cervical plane. On this plane, I measured two intersected angles as follows

(Figure 3, Table 1): (1) buccal surface angle (BSA); and (2) lingual surface angle (LSA). BSA is formed by the intersection of the line which connects the lowest point of the DEJ on the buccal side and the apex of the enamel tip of the protoconid, and the line which passes through the lowest points of the DEJ on the buccal and lingual sides (the cervical line). LSA is formed by the intersection of the line which connects the lowest point of the DEJ on the lingual side and the apex of the enamel tip of the metaconid, and the cervical line.

Five linear measurements are used in this study as follows (Figure 3, Table 1): (1) mesial width along the cervical plane (MCW); (2) height of the mesio-buccal cusp or protoconid (MBCH); (3) enamel thickness on the lingual slope of the protoconid (ETLP); (4) enamel thickness on the buccal slope of the protoconid (ETBP); and (5) enamel thickness on the cusp tip of the protoconid (ETCP). MCW is a distance between the lowest points of the DEJ on the buccal and lingual sides. MBCH is a minimum distance between the cusp tip of the protoconid and the cervical plane. ETLP is a linear thickness from the dentine horn of the protoconid perpendicular to the outer enamel surface on the lingual slope of the protoconid. ETBP is a linear thickness perpendicular to the DEJ on the buccal slope of the protoconid at 0.5mm from the dentine horn of the protoconid. ETCP is a distance between the cusp tip and the dentine horn of the protoconid.

To evaluate enamel thickness, four landmarks were defined on the buccal DEJ surface of the tooth at different levels (Figure 4). Each landmark was intersected by lines that were parallel with the cervical line (B-L) and the buccal DEJ surface. Landmark 1 (LMK1): at the level of the horn apex of protoconid. Landmark 2 (LMK2): through the lowest point of intercuspul fissure on OES. Landmark 3 (LMK3): through the lowest level of the DEJ between the buccal and lingual dentine horns (O-P). Landmark 4 (LMK4): at the mid-level between the cervical line B-L and the line O-P.

The distribution of enamel on the buccal side was measured in two ways. The enamel thickness (ET) was measured perpendicular to DEJ from LMK2, LMK3 and LMK4 (Figure 5). The reason for measuring the ET is for comparison with the distribution of enamel on the buccal surface of M_2 in *P. badius* and *M. fuscata*.

The enamel rim width (ERW) was measured as the thickness at each reference point with an elevation of 16.2° in *P. badius*, and 12.4° in *M. fuscata* from the cervical line. The ERW evaluates the thickness of the enamel rim in different tooth wear stages (Figure 6). When the buccal cusps are worn and dentine is exposed, flattened enamel rims form around the dentine exposure. The angles used for ERW were measured by the following method. I observed that the angle of the enamel rim relative to the cervical line has a sexual and interspecific difference between *P. badius* and *M. fuscata*, and this relates to the stage of tooth wear. Thirty-seven M_2s of *Procolobus badius* and thirty M_2s of *Macaca fuscata* in various stages of tooth wear were used. These were from free-ranging individuals. The *P. badius* sample consisted of 19 males and 18 females housed in the American Museum of Natural History, New York. The *M. fuscata* sample consisted of 12 males and 18 females housed at the Primate Institute of Kyoto University, Inuyama. Epoxy casts were made of M_2s of *P. badius* and *M. fuscata*. These casts were sectioned through the buccal ridge and lingual ridge of the mesial cusps perpendicular to the base of the crown. Each cut face was photographed, and the image was used to measure the angle in a personal computer. Tooth wear stages were examined using Gantt's (1979) scale for assessing enamel attrition in cercopithecoids. The results demonstrate that there is no significant sexual difference and no relationship between wear stage and the degree of angulation, but a significant interspecific difference in this angle. The occlusal surface of the enamel rim has an angle of 16.2° in *P. badius* and 12.4° in *M. fuscata*.

For partly worn teeth, measurements affected by wear were excluded from the analyses. Since there is a difference in molar size between *P. badius* and *M. fuscata* all linear measurements were normalized by the value of MCW. The Student's t-test was used to examine interspecific differences. The paired t-test was used to compare enamel thickness (ET) and enamel rim width (ERW) in *P. badius* and *M. fuscata*.

Results

Basic statistics on the mesial width along the cervical plane (MCW), buccal surface angle (BSA), and lingual surface angle (LSA) are given in Table 2. A significant interspecific difference was found in MCW. The MCW of *P. badius* was 5.1 mm and that of *M. fuscata* was 6.6 mm. Interspecific difference was found in the BSA, but not in the LSA. *Procolobus badius* had a greater BSA (72.0°) whereas *M. fuscata* had a much lower value (54.7°). The LSA of both species was slightly greater than 90°. The greater the BEA, the more buccally positioned the protoconid. Thus, the BSA is a measure of the flare of the crown on the buccal side. Larger angles of BSA indicate that the crown is less flared and smaller angles more flared. Molars of *P. badius* were less flared than those of *M. fuscata*. An LSA at right angles indicates that flare was only observed on the buccal side in both species (Table 2). The buccal cusps in the less flared *P. badius* molars are positioned closer to the margins of the tooth than in *M. fuscata*, with *P. badius* having longer shearing crests and lophs than *M. fuscata*. Longer shearing crests are associated with a higher proportional intake of leaves (Kay, 1978; Kay & Hylander, 1978).

All of the linear measurements (height of mesio-buccal cusp, MBCH; enamel thickness on the buccal slope of protoconid, ETBP; enamel thickness on the lingual slope of protoconid, ETLP; and enamel thickness on the cusp tip of protoconid, ETCP) presented in Table 3 are significantly different between the two species. The relative MBCH in *P. badius* (98.9) was higher than in *M. fuscata* (80.3). All the relative enamel thicknesses on the protoconid (ETBP, ETLP, ETCP) were thinner in *P. badius* than in *M. fuscata*. Relative enamel thickness on the buccal side (ETBP) was 11.1 in *P. badius* and 15.4 in *M. fuscata*, while that on the lingual side (ETLP) was 2.5 in *P. badius* and 7.4 in *M. fuscata*. This coincides with the fact that dentine exposure is observed earliest on the latter part of the crown. The CET was larger in *M. fuscata* regardless of the almost vertically aligned cusp tip and the dentine horn. In addition, the proportions of enamel thickness in these areas differed in the two species. The difference between ETBP or ETCP and ETLP of *P. badius* was larger than in *M. fuscata*. The ETBP part of the protoconid corresponds to facet 1 or facet 2 of Phase I, and the ETLP part of the protoconid corresponds to facet x or facet 10n of Phase II of the power stroke of mastication (Kay, 1977). Phase I mastication relates predominantly to shearing activities, while Phase II relates to crushing and grinding activities. The ETCP part of the protoconid functions for tip crushing during the puncture-crushing phase of the masticatory cycle (Hiiemae, 1978; Janis, 1984).

Data on enamel thickness (ET) and enamel rim width (ERW) are shown in Tables 4 & 5. *Procolobus badius* has thinner enamel on the buccal surface of the protoconid near the cusp tip (LMK2). The relative ET of *P. badius* was 12.7 at LMK2 level and *M. fuscata* was 15.8. However, enamel thickness did not differ significantly at other levels.

The pattern of enamel distribution on *P. badius* molars was characterized by enamel thickness that was distributed equally at the level of LMK2 – LMK3, in which the difference was only 0.1, while the decrease at the level of LMK3 – LMK4 was 3.3. Furthermore, the enamel thickness at the ETBP level was 11.1, slightly thinner than at the mid-level of the buccal surface. In contrast, in *M. fuscata* the enamel thickness at the ETBP and LMK2 is distributed uniformly; the ETBP was 15.4 and the ET at LMK2 was 15.8. After that, enamel thickness decreases gradually from LMK2 to LMK4. The change in enamel distribution between LMK3 and LMK4 was greater than that between LMK2 and LMK3.

The ERW exhibited a different pattern. The results indicate that *P. badius* had a narrower enamel rim than *M. fuscata* at three of the four levels on the buccal surface of the protoconid. The relative ERWs of *P. badius* at LMK1 to LMK3 levels were 11.6, 12.0, and 11.9

respectively, while those of *M. fuscata* were 19.9, 19.0, and 13.6 respectively.

Raw values of the ETs and ERWs are compared in Table 6 and Figure 7. In *P. badius*, the ERWs have comparable values with the ETs at all levels. On the other hand, in *M. fuscata* ERWs were significantly larger than the ETs at two mid levels (at LMK2 and LMK3). The ERW of *P. badius* exhibits slight change through the different levels. In *P. badius* the ERWs have the same values through LMK1 to LMK3, while the range of the ERW (maximum – minimum) through LMK1 to LMK3 is as much as 0.3 mm in *M. fuscata*. It should be noted that *P. badius* maintains a constantly narrow buccal enamel rim as molar crown attrition progresses.

Discussion

In several studies, enamel thickness distribution has been discussed in relation to the hypothesis that loading areas of the molar crown possess thicker enamel than non-loading areas (Gantt, 1977; Molnar & Gantt, 1977; Martin, 1983; Grine & Martin, 1988; Macho & Thackeray, 1992). The different pattern of enamel distribution observed in the two species studied here are consistent with this hypothesis. However, loading on the lingual slope of the protoconid in *P. badius* seems lower than that on the buccal slope; the ETLP is too thin to resist wear. Facet x and facet 10n are produced by direct contact with the corresponding facet on the upper molars during Phase II of mastication.

The earliest dentine exposure on lower molars is observed on the lingual slope of the protoconid in *P. badius*. The thinner enamel in this area seems contradictory to tooth function maintenance. However, if thin enamel is presumed to contribute to rapid exposure of the dentine in this area in order to form sharp enamel rims on the buccal side of the protoconid, this feature is functionally adapted for processing fibrous foods. Attrition of the lower molars begins as a round depression at the protoconid tip, and eventually enamel is removed from the tip of the protoconid to form a flat surface, as shown in pig-tailed macaque (*Macaca nemestrina*), rhesus macaque (*Macaca mulatta*) and yellow baboon (*Papio cynocephalus*) (Gantt, 1979). Wear on the lower molars in *M. fuscata* follows this pattern. After that, the dentine is exposed at the center of the flattened enamel. Due to the thick enamel on the protoconid, occlusal relief can easily be reduced to a flat surface without dentine exposure, thereby forming a wide grinding facet.

Differences in the ET, the BSA and the angle of enamel rims relative to the cervical plane, reflect differences in the area of the enamel rim that surround the dentine patches on the cusp tips; the ET and the ERW are both greater. When the enamel rims meet the buccal slope of the molar crown at a right angle, ERW has the narrowest values. As this angle becomes more acute or obtuse, ERW becomes thicker. Because the angle in *P. badius* approximates a right angle (88.2°) and the enamel is thinner, *P. badius* can maintain as narrow enamel rims as possible. The ERWs have comparable value with the ETs at all levels. Another unique feature is the constant thickness of the enamel rim through different levels. In other words, the enamel rim remains narrow as wear progresses. A narrow enamel rim is apparently less adaptive for crushing and grinding of hard objects, but may be effective for shearing and shredding fibrous foods in folivores. It has been shown that colobines can process leaves into smaller pieces within a shorter period of time than can cercopithecine monkeys (Walker & Murray, 1975).

On the other hand, in *M. fuscata* the angle formed by the enamel rims and the buccal slope of the molar crown is 67.1° and the enamel is thicker, such that *M. fuscata* possesses wider enamel rims relative to ET. In fact, ERWs are 20% greater at LMK2 compared with ET, and 10% greater at LMK3. *Macaca fuscata* not only has thick enamel on the buccal slope of the protoconid, but also pronounced flare of the molar crown. As a result, the enamel rim of *M. fuscata* is wider than the enamel thickness on the buccal slope of the protoconid. All of these features permit the enamel rim to function as an effective surface for food crushing and grinding.

The thinner enamel on the buccal slope is associated with more rapid progress of tooth wear. Microwear studies show that harder foods lead to faster rates of wear in *Cercopithecus aethiops* (Teaford & Oyen, 1989). The folivorous *P. badius,* which processes more leaves than the omnivorous *M. fuscata,* produces heavier loading on its molars along with quicker enamel wear. *Procolobus badius* has much higher molar crowns than *M. fuscata* (Table 2, MBLH), presumably to compensate for this faster wear.

The following three characters of *P. badius* lower molars indicate that the enamel rims provide an efficient shearing mechanism for a longer period: (1) the enamel is thin and uniformly distributed on the buccal slope of the molar crown at the level of ETBP, LMK2 and 3; (2) the width of the enamel rims are as narrow as possible, because the buccal slope of the molar crown is very steep, and the angle between the enamel rims and the buccal slope approximates a right angle; and (3) the crown is high. As the enamel rims are formed easily, enamel on the lingual slope of the protoconid is considerably thinner than on the buccal slope of the protoconid. After dentine exposure, the narrow enamel rims do not function as crushing/grinding facets, but as shearing crests. It is presumed that the worn molars of adult red colobus monkeys function more efficiently for shearing than do the unworn molars of subadult individuals.

Summary

The purpose of this paper was to compare the enamel distribution pattern on the molars of the folivorous *P. badius* and omnivorous *M. fuscata*, and to try to relate the observed difference with their dietary behavior. Comparisons focused on the enamel distribution on the buccal slope in relation to enamel rims that form on the buccal side after dentine exposure. The lingual slope of the protoconid wears faster than other occlusal surfaces on the lower molars of *P. badius*, as the enamel in this region is very thin. By contrast, in *M. fuscata* the enamel on the cusp tip of the protoconid is thick, and dentine exposure is delayed. *Procolobus badius* has undeveloped crown flare, thin enamel on the buccal slope of the molar crown, and high-crowned molars. This combination of attributes produces enamel rims surrounding the dentine exposure on the buccal cusps that keep the same width and sharp edges during an extended period of their life. In contrast, *M. fuscata* has well-developed crown flare and thick enamel on the buccal slope of its lower molar crowns. Consequently, the enamel rims of their molars are wide after dentine exposure. In *P. badius* the morphology of the buccal slope of the crown serves to maintain the functions of shredding and shearing as wear progresses, while the enamel rims of *M. fuscata* are structurally most effective for crushing and grinding.

Acknowledgments

I thank Prof. Hidemi Ishida, Dr. Masato Nakatsukasa and other staff of the Laboratory of physical anthropology, Kyoto University for their helpful suggestions and insightful comments. Dr. Hironori Takemoto of Advanced Telecommunication Research Institute International helped me analyse the CT data. I acknowledge helpful discussions with Dr. Yuzuru Hamada, Dr. Toshio Mouri, Dr. Yutaka Kunimatsu, Mr. Takeshi Nishimura and Ms. Michika Kondo of the Primates Research Institute, Kyoto University. My special thanks are due to Dr. Richard Kay of Duke University for valuable advice. This paper was much improved with the help of comments from three anonymous reviewers.

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Table 1. List of linear measurements (see Figure 3)

	Dimension	Definition
BSA:	Buccal surface angle	Angle formed by the ntersection of the line which connects the lowest point of the DEJ on the buccal side and the apex of the enamel tip of the protoconid, and the line which passes through the lowest points of the DEJ on the buccal and lingual sides.
LSA:	Lingual surface angle	Angle formed by the intersection of the line which connects the lowest point of the DEJ on the lingual side and the apex of the enamel tip of the metaconid, and the line which passes through the lowest points of the DEJ on the buccal and lingual sides.
MCW:	Mesial width	Distance between the lowest points of the DEJ on the of the cervical planebuccal and lingual sides.

(continue to next page)

(table 1; continue from previous page)

	Dimension	Definition
MBCH:	Height of the protoconid	Minimum distance between the cusp tip of the protoconid and the cervical plane
ETLP:	Enamel thickness on the lingual slope of the protoconid	Linear thickness from the dentine horn of the protoconid perpendicular to the outer enamel surface (OES) on the lingual slope of the protoconid.
ETBP:	Enamel thickness on the buccal slope of the protoconid	Linear thickness perpendicular to the DEJ on the buccal slope of the protoconid at 0.5mm from the dentine horn of the protoconid.
ETCP:	Enamel thickness on the cusp tip of the protoconid	Distance between the cusp tip and the dentine horn of the protoconid.

Table 2. Comparison of *Procolobus badius* and *Macaca fuscata* in the mesial width on the cervical plane (MCW), angle of buccal slope (BSA), angle of lingual slope (LSA) using Student's t-test

Species	MCW (mm)	BSA (degrees)	LSA (degrees)
P. badius			
mean	5.1	72.0	97.4
S.D.	0.54	5.34	4.25
N	8	8	7
M. fuscata			
mean	6.6	54.7	94.9
S.D.	0.43	2.89	2.98
N	6	6	6
T-value	-5.62	7.12	1.21
significance	***	***	

Three asterisks indicates that $p<0.001$

Table 3. Comparison of *Procolobus badius* and *Macaca fuscata* in the relative height of the protoconid (MBCH), enamel thickness on the buccal slope of the protoconid (ETBP), enamel thickness on the cusp tip of the protoconid (ETCP), enamel thickness on the lingual slope of the protoconid (ETLP) using Student's t-test

Species	MBCH	ETBP	ETCP	ETLP
P. badius				
mean	98.9	11.1	6.8	2.5
S.D.	13.79	2.05	0.63	0.34
N	8	8	8	7
M. fuscata				
mean	80.3	15.4	13.0	7.4
S.D.	5.44	1.02	0.76	0.76
N	6	6	6	6
T-value	3.11	-4.71	-19.62	-15.48
significance	**	***	***	***

Two asterisks indicates that $p<0.01$, and the three asterisks that $p<0.001$.

Table 4. Comparison of *Procolobus badius* and *Macaca fuscata* in the relative enamel thickness using Student's t-test

Landmarks	2	3	4
P. badius			
mean	12.7	12.6	9.3
S.D.	1.74	2.45	2.10
N	8	8	8
M. fuscata			
mean	15.8	13.1	8.1
S.D.	1.54	0.68	1.09
N	6	6	6
T-value	-3.49	-0.51	1.28
significance	**		

Two asterisks indicates that $p<0.01$.

Table 5. Comparison of *Procolobus badius* and *Macaca fuscata* in the relative enamel rim width using Student's t-test

Landmarks	1	2	3	4
P. badius				
mean	11.6	12.0	11.9	8.9
S.D.	1.36	1.59	1.16	1.68
N	8	8	8	8
M. fuscata				
mean	19.9	19.0	13.6	8.4
S.D.	2.60	1.77	0.66	1.24
N	6	6	6	6
T-value	-7.89	-7.54	-5.24	0.69
significance	***	***	***	

Three asterisks indicates that $p<0.001$.

Table 6. Comparison of enamel thickness (ET) and enamel rim width (ERW) (mm) in *Procolobus badius* and *Macaca fuscata* using paired t-test.

	P. badius				*M. fuscata*			
Landmarks	1	2	3	4	1	2	3	4
ET								
mean		0.6	0.6	0.5		1.1	0.9	0.5
S.D.		0.07	0.09	0.07		0.10	0.08	0.08
N		8	8	8		6	6	6
ERW								
mean	0.6	0.6	0.6	0.4	1.3	1.2	1.0	0.6
S.D.	0.06	0.10	0.08	0.07	0.16	0.10	0.05	0.05
N	8	8	8	8	6	6	6	6
T-value		0.68	1.00	1.53		-5.97	-2.74	-0.42
significance						**	*	

One asterisk indicates that $p<0.05$, two asterisks that $p<0.01$.

Legends of Figure

Figure 1. CT number profile in a linear trace through a cross-section CT image of a red colobus molar. The boundaries between enamel, dentine and air were determined by the method of HMH. (see text for further details)

Figure 2. A part of the CT number matrix including the enamel-dentine boundary and the enamel-air boundary.

Figure 3. Cross-section through the mesial cusps of a mandibular molar showing (a) the two angles – BSA and LSA; (b) the four linear measurements – MCW and MBCH, and (c) ETLP, ETBP and ETCP.

Figure 4. The reference points for measuring the enamel thickness and the enamel rim width. LMK1 is defined as the dentine horn of the protoconid. And the other points are defined as the intersections on the buccal DEJ surface of tooth crown relative to a line parallel to the crown base (line B-L) through the lowest point of intercuspul fissure (line Q-R) for LMK2, the lowest point of DEJ between cusps (line O-P) for LMK3, and the midpoint of the line O-P and the line B-L (line M-N) for LMK4.

Figure 5. Cross-section through the mesial cusps showing three dimensions of the enamel thickness (ET2 – 4). All measurement are perpendicular to the DEJ from LMK2 – 4.

Figure 6. Cross-section through the mesial cusps showing the definition of the enamel rim width (ERW). The enamel rim formed after dentine exposure has an angle relative to the cervical plane of: (a) θ is the angle of the enamel rims relative to the cervical plane; (b) 16.2° (–) for red colobus;

(c) 12.4° (=) for Japanese macaque.

Figure 7. Distribution profile of generalized enamel thickness (ET) and enamel rim width (ERW) at each reference point. Symbols show mean values and vertical bars indicate one standard deviation. Pb = *Procolobus badius*; Mf = *Macaca fuscata*.

Figure 1

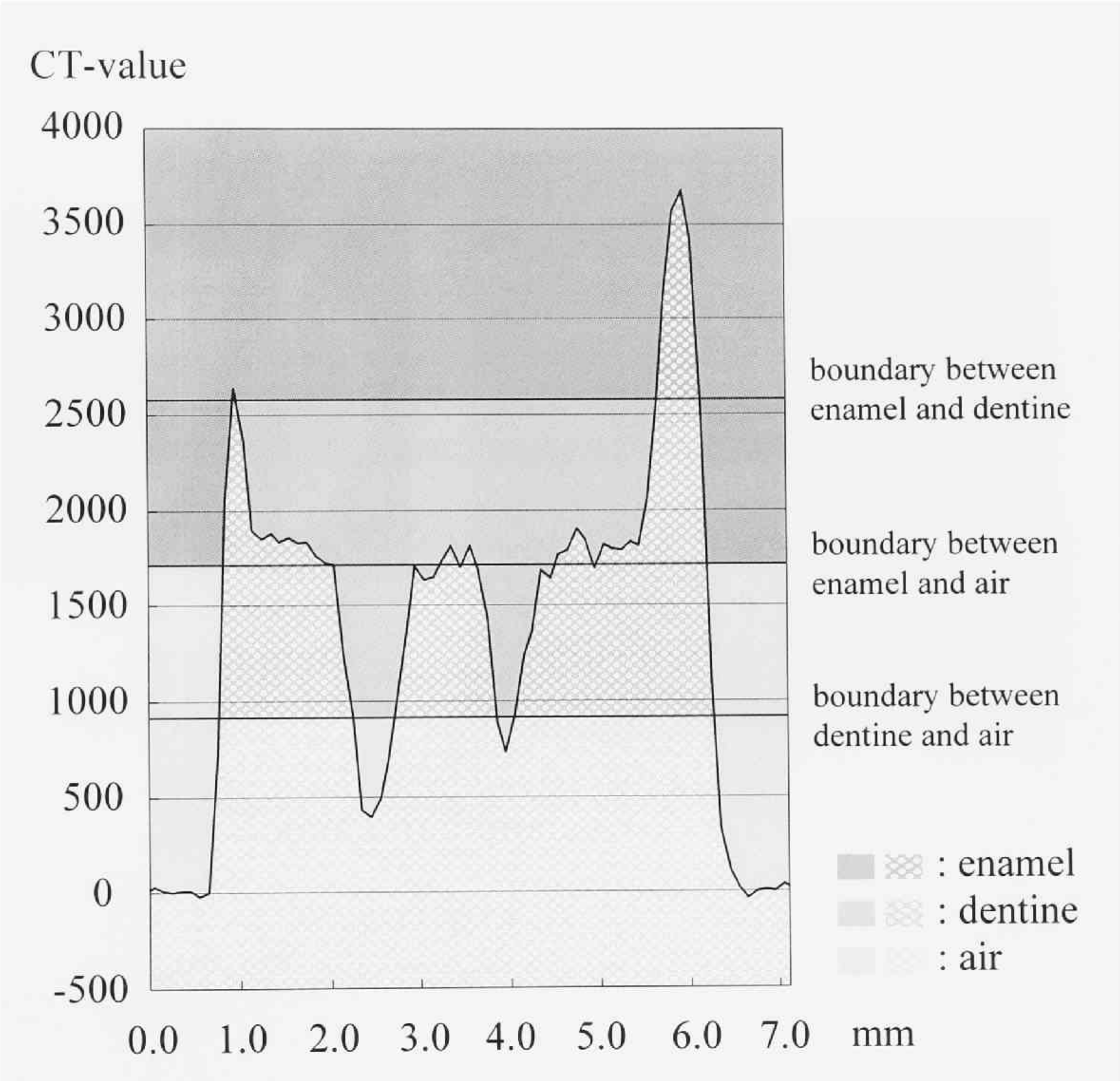
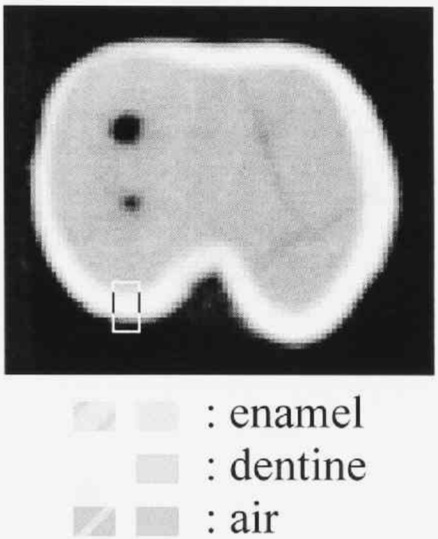
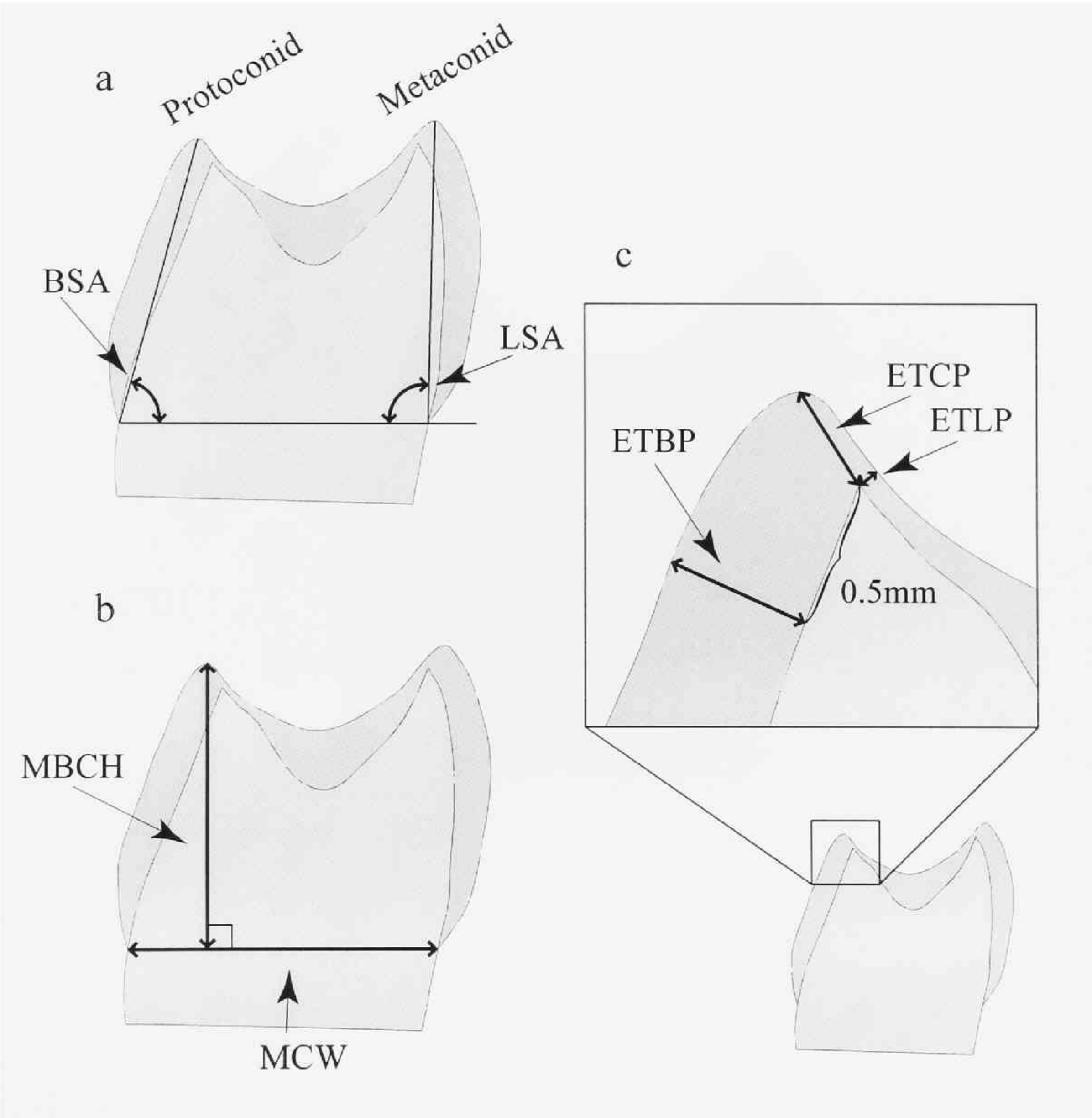

CT-value
4000
3500
3000
2500
2000
1500
1000
500
0
-500
0.0 1.0 2.0 3.0 4.0 5.0 6.0 7.0 mm
boundary between enamel and dentine
boundary between enamel and air
boundary between dentine and air
: enamel
: dentine
: air

Figure 2



2089	2029	2013	2067	2176
2481	2470	2432	2564	2827
3083	3131	3113	3130	3191
3620	3564	3590	3573	3514
3641	3570	3685	3673	3477
3523	3579	3520	3428	3396
2425	2587	2626	2525	2445
974	1016	1081	1096	977
348	293	350	333	364
133	130	73	110	86

Figure 3



a
Protoconid
Metaconid
BSA
LSA
b
MBCH
MCW
c
ETCP
ETLP
ETBP
0.5mm

Figure 4

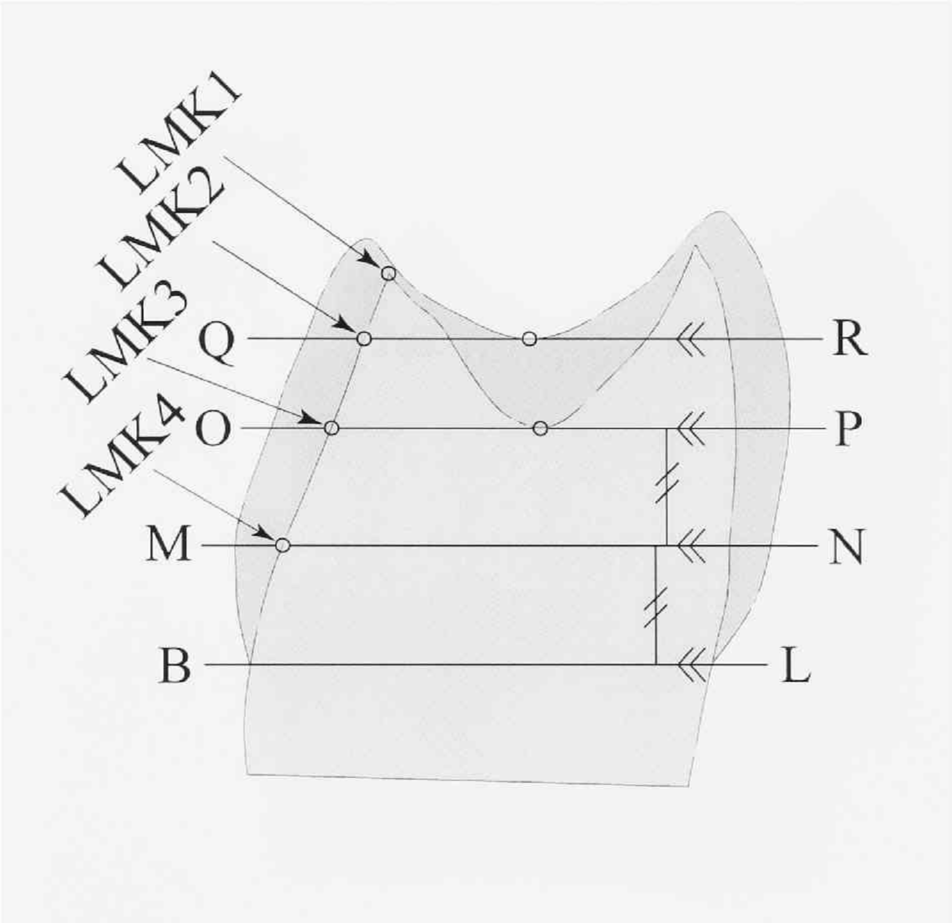


Figure 5

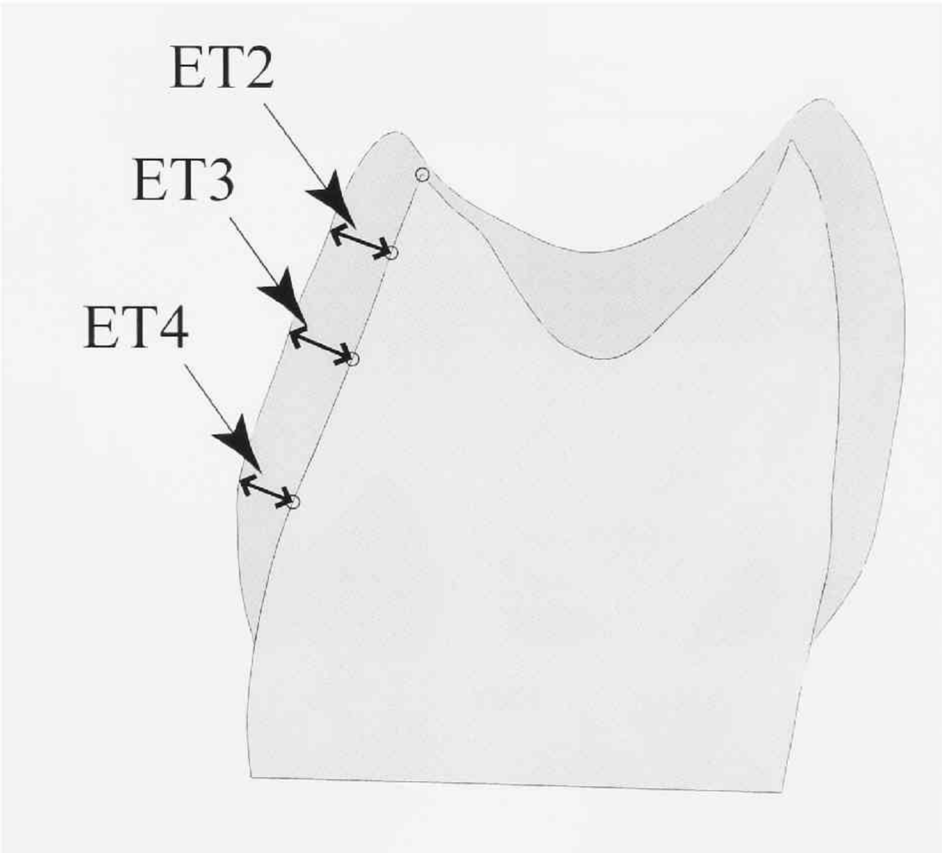


Figure 6

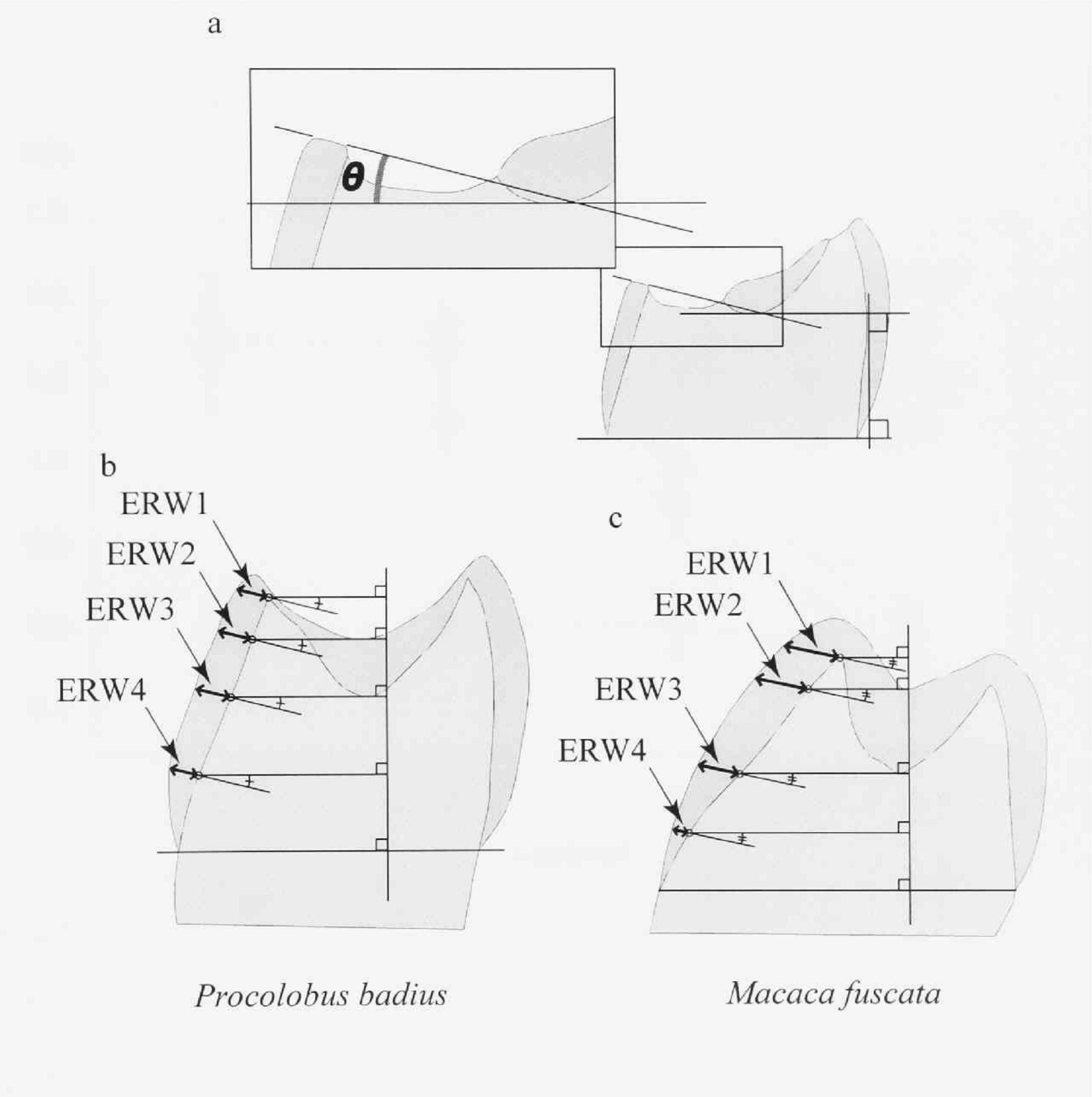

a
θ
b
ERW1
ERW2
ERW3
ERW4
c
ERW1
ERW2
ERW3
ERW4
Procolobus badius
Macaca fuscata

Figure 7